The relationship between intraspecific assortative mating and reproductive isolation between divergent populations

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Abstract The term ‘assortative mating’ has been applied to describe two very different phenomena: (1) the tendency for individuals to choose phenotypically similar mates from among conspecifics; or (2) the tendency to prefer conspecific over heterospecific mates (behavioral reproductive isolation). Both forms of assortative mating are widespread in nature, but the relationship between these behaviors remains unclear. Namely, it is plausible that a preference for phenotypically similar conspecifics incidentally reduces the probability of mating with phenotypically divergent heterospecifics. We present a model to calculate how the level of reproductive isolation depends on intraspecific assortative mating and the phenotypic divergence between species. For empirically reasonable levels of intraspecific assortment on a single trait axis, we show that strong reproductive isolation requires very substantial phenotypic divergence. We illustrate this point by applying our model to empirical data from threespine stickleback Gasterosteus aculeatus and Darwin’s Finches (Geospiza spp). We conclude that typical levels of intraspecific assortment cannot generally be extrapolated to explain levels of interspecific reproductive isolation. Instead, reproductive isolation between species likely arises from different mate choice behaviors, or multivariate assortative mating [Current Zoology 58 (3): 484–492, 2012].

Keywords Assortative mating, Hybridization, Mating preference, Reproductive isolation, Speciation

Assortative mating is the tendency for individuals to select mates who are phenotypically more (or less) similar to themselves than expected by chance (Wright 1921; Arnqvist et al., 1996). This non-random mating can be observed both within and between populations or species. For example, within a single population of threespine stickleback Gasterosteus aculeatus, males and females tend to pair with ecologically similar mates, leading to a positive phenotypic correlation between mated pairs (Snowberg and Bolnick, 2008). Non-random mate choice is also observed between divergent allopatric populations (Rundle et al., 2000; Vines and Schluter, 2006), and between sympatric species pairs (Rundle and Schluter, 1998; Boughman, 2001; Rafferty and Boughman, 2006; Kozak et al., 2009). An important but unresolved question is whether these different types of non-random mating (within and between populations or species) are caused by a shared mechanism. Specifically, is reproductive isolation between species an emergent consequence of positive assortative mating within populations (Ryan and Rand, 1993)?

If individuals select phenotypically similar mates from within their own population, the same mating preferences may reduce the probability of mating with individuals from a phenotypically divergent population or species. This scenario is assumed in numerous models of speciation in which disruptive selection drives the evolution of increased assortative mating (e.g., Dieckmann and Doebeli, 1999; Kirkpatrick and Ravigne, 2002; Gavrilets, 2003, 2004; Bürger et al., 2006; de Cara et al., 2008). Alternatively, reproductive isolation between species might arise from different (or additional) behavioral barriers to mating. Surprisingly, despite numerous studies of both assortative mating (Johnston and Johnson, 1989; Arnqvist et al., 1996; Bernstein and Bernstein, 2003; Cézilly, 2004; Pryke and Griffith, 2007; Jiang et al., Manuscript) and reproductive isolation between populations (Coyne and Orr, 2004), it is unclear whether intraspecific assortative mating can be extrapolated to explain levels of interspecific reproductive isolation.

The goal of this paper is to evaluate the conditions in which intraspecific assortment can generate strong reproductive isolation between species. We calculate the level of reproductive isolation between populations, for a given level of intraspecific assortative mating and phenotypic divergence between the populations. We then ask how divergent two populations must be to attain strong reproductive isolation, given empirically reasonable levels of intraspecific assortment.
1 Model

Reproductive isolation between two species depends on the rate of hybridization in each reciprocal cross direction. Here, we focus on the level of reproductive isolation arising from one cross direction, by calculating the probability that a female of species 1 mates with a conspecific male as opposed to a heterospecific male of species 2. We assume that (i) females of focal species 1 choose their mates on the basis of a single quantitative trait that is expressed in both sexes, (ii) all females have an equal probability of mating, and (iii) males mate polygynously and are not choosy.

The probability that a female of the focal species mates with a conspecific is

\[ p_c = \int p_1(y) \left( \frac{m_1(z|y)}{m_1(z|y) + m_2(z|y)} \right) dz \quad (1) \]

where \( p_1(y) \) is the frequency of females with phenotype \( y \) in the focal species 1, and \( m_i(z|y) \) is the probability that a focal-species female with phenotype \( y \) mates with a species \( i \) male (where \( i \in \{1, 2\} \) with phenotype \( z \):

\[ m_i(z|y) = f_i p_i(z) \psi(z|y) k(y) \quad (2) \]

Here \( f_i \) is the total frequency of species \( i \) in the environment where mating occurs (that is, among all individuals of both species), which affects the frequency with which individuals encounter potential conspecific mates. The term \( p_i(z) \) is the frequency of males with phenotype \( z \) within species \( i \), and \( \psi(z|y) \) is the mating preference of a female with phenotype \( y \) for a male with phenotype \( z \). Last, \( k(y) \) is a normalizing factor that assures all females have equal probability of mating, but it cancels in Eq. (1) and so its value is not important to our calculation.

To this point we have not made any assumptions about the phenotypic distributions of the two species or the form of the mating preference function. We now assume that female choose males assortatively based on an absolute mating preference function (Lande 1981):\n
\[ \psi(z|y) = \exp \left\{ -\frac{(z-y)^2}{2\omega^2} \right\} \quad (3) \]

Females have strongest preference for males that match their phenotype (\( z = y \)), and their preference falls off as a Gaussian function as the male and female phenotypes diverge. The parameter \( \omega^2 \) measures how rapidly the preference falls off: small values of \( \omega^2 \) correspond to strong preferences and hence strong assortment, while large values of \( \omega^2 \) imply the converse. Our final assumption is that the phenotypic distributions of each species are normal and have equal variance. It is convenient to measure the trait on a scale such that this variance equals 1. We denote the difference between the phenotypic means of the two species as \( \Delta \), measured in phenotypic standard deviations. We assume that the two species evolved their phenotypic differences in allopatry, and subsequently come into secondary contact.

Substituting Eqs. (2–3) into (1) gives the probability of conspecific mating. It is not possible in general to find a closed form solution for that expression. We can, however, solve the equation numerically for any specific case of interest. The conclusions presented in the Results section are based on numerical solutions implemented in R (R Development Core Team 2007). It is, however, worth noting that one can find approximations for some special cases. In the case of weak mating preferences (\( \omega^2 >> 1 \)) it is straightforward to show that the probability of conspecific mating is approximately

\[ p_c \approx \frac{f_1}{f_1 + (1-f_1) \exp\left\{ -\Delta^2 / 2\omega^2 \right\}} \quad (4) \]

Comparisons of this approximate \( P_c \) to the values calculated by numerical integration reveal that the approximation is quite close when the phenotypic correlation between mates is small (\( r < 0.1 \)), but appreciably overestimates \( P_c \) when \( r > 0.2 \) and/or when \( f_1 \) is small.

The parameters that determine the probability of conspecific mating in our model are \( \Delta \) (the number of standard deviations between the means of the two species), \( f_1 \) (the frequency of the focal species), and \( \omega^2 \) (the width of the preference function relative to the phenotypic variance). The first two parameters are relatively simple to estimate in nature, but the third is not. Consequently, we next replace \( \omega^2 \) with a more empirically tractable measure, the phenotypic correlation between mated pairs within a species, \( r \). Hall et al. (2000) calculated the relationship between \( \omega^2 \) and \( r \), assuming the preference function described above (Eq. 3) for normally distributed phenotypes. Rearranging their equation (Table 1 of Hall et al. 2000) and assuming equal trait variance in males and females, gives

\[ \omega^2 = \sqrt{\frac{1-r^2}{r^2}} \quad (5) \]

This expression can be substituted into Eq. (3) (for the general case) and Eq. (4) (when preferences are weak). The appeal of parameterizing our model in terms of \( r \) rather than \( \omega^2 \) is that \( r \) has been estimated for many natural populations (Jiang et al. In revision).

We used numerical integration to calculate the probability of conspecific mating for a range of parameter value combinations. We examined assortative mating...
strength ranging from $r = 0.001$ to 0.5 (in increments of 0.01), spanning the majority of empirical measures. Each male-female correlation was converted into a measure of mate preference strength ($\omega^2$; eq. 5). We considered interspecific divergence levels ranging from 0 to 20 phenotypic standard deviations, in increments of 0.2. Finally we considered cases where the focal species is rarer, equally abundant, and more common than the heterospecific species ($f_1 = 0.1, 0.5, \text{ or } 0.9$).

2 Results

The probability of conspecific mating is a monotonically increasing function of the strength of assortative mating within the focal species ($r$, inversely related to $\omega^2$), and of the phenotypic difference $\Delta$ between species (Fig. 1). When the species are identical ($\Delta = 0$) or mate randomly with respect to phenotype ($r = 0$), the probability of conspecific mating depends solely on the relative frequency of the two species ($P_c = f_1$). Increasing the strength of assortative mating ($r$) has little effect on $P_c$ when the two populations are phenotypically very similar (e.g., $\Delta < 5$; Fig. 1). For more substantially diverged populations (e.g., $\Delta > 10$), increasing assortative mating from $r = 0$ to approximately $r \sim 0.1$ leads to a rapid increase in reproductive isolation approaching $P_c > 0.95$; further increases in assortative mating have little additional effect on $P_c$. Species’ relative frequencies ($f_i$) have little effect on the level of reproductive isolation when species are strongly isolated due to large phenotypic differences and moderate to strong assortative mating (Fig. 1).

Another way to examine our model is to determine how phenotypically divergent two populations must be to attain a given level of reproductive isolation (Fig. 2). Obviously, populations must be more divergent to attain more stringent isolation. The minimum divergence is quite large for weak assortative mating ($r < 0.05$), but rapidly decreases with small increases in assortative-mating (Fig. 2). For example, to achieve 95% reproductive isolation, populations must be ~16 standard deviations.

Fig. 1 The probability of conspecific mating as a function of the distance between the mean phenotypes of two co-occurring species ($\Delta$, measured in units of standard deviations) and the strength of assortative mating within a focal species ($r$, the phenotypic correlation between mates)

The three panels correspond to increasing frequency of the focal species (A) $f_1 = 0.1$; (B) $f_1 = 0.5$; (C) $f_1 = 0.9$. 
apart when \( r = 0.025 \) (assuming \( f_1 = 0.5 \)), but only 8.8 standard deviations apart when \( r = 0.1 \) (Fig. 2). Further increasing assortment only moderately changes the required divergence for 95% isolation (e.g., \( r = 0.2 \) requires \( \Delta > 6.9 \) and \( r = 0.5 \) requires \( \Delta > 5.1 \)). As \( r \) increases towards 1, the level of reproductive isolation asymptotically approaches a maximum level of reproductive isolation, determined by the area of overlap between the two species’ trait distributions.

Fig. 2  The minimum phenotypic difference between species (measured in standard deviations) required to achieve a specified level of reproductive isolation (\( RI = P_{con} = 0.95, 0.99 \) and 0.999), as a function of the strength of intraspecific assortative mating (\( r \))

The average strength of assortative mating from the meta-analysis of Jiang et al. (in revision) is indicated with a bold arrow. The light arrow indicates the average of the cases of positive assortative mating (e.g., only considering those cases where \( r > 0 \)). The two species are assumed to be equally common, and have identical trait variances.

Our calculations show how the degree of interspecific isolation varies with the strength of within-species assortment. What then is a typical strength of assortment? Jiang et al. (Manuscript) collected 1118 estimates of assortative mating from 254 species distributed across 5 phyla. Estimates of assortative mating (the phenotypic correlation \( r \) between mated pairs) varied widely, with an average of \( r = 0.27 \) (significantly different from zero). The majority of correlation coefficients (81.5%) fall in the range \( 0 < r < 0.5 \). Assuming strong but realistic assortative mating (\( r = 0.5 \)) and assuming equal species abundance, our results show that the populations’ means must be at least 5.1 standard deviations apart to reduce hybridization rates to 5% (\( P_e = 0.95 \); Fig. 2). To reduce hybridization to 1% or 0.1% of matings requires that the populations be, respectively, 6.6 or 8.4 standard deviations apart.

To place our theoretical results in an empirical context, it is helpful to examine a few cases where biologists have measured both intraspecific assortment and phenotypic divergence between co-occurring sister species. Specifically, we can ask whether phenotypic divergence between sympatric species pairs is sufficient to explain their reproductive isolation, for reasonable levels of assortment on a single trait. This requires information on the strength of intraspecific assortment, reproductive isolation between species, and phenotypic divergence between species.

Case study 1: Threespine stickleback

Assortative mating has been documented within single-species lake populations of threespine stickleback *Gasterosteus aculeatus*: there is a correlation of \( r = 0.282 \) between the trophic position (measured by nitrogen stable isotope ratios, \( \delta^{15}N \)) of mated male and female pairs in Browns Bay Lake, British Columbia (Snowberg and Bolnick In review), and \( r = 0.53 \) in nearby Little Goose Lake (Snowberg and Bolnick 2008). Adopting the average of these two estimates (\( r \approx 0.4 \)), our model suggests that this intraspecific assortment could reduce hybridization rates to below 5% if co-occurring species are at least 5.4 standard deviations apart. Five percent hybridization is an appropriate cutoff given that hybrids are observed between stickleback species pairs at slightly below this frequency (Schluter and McPhail, 1992). For comparison, the co-occurring benthic and limnetic species pairs are only 0.6 standard deviations apart with respect to trophic position (\( \delta^{15}N \); Matthews et al., 2010). Consequently, the assortative mating observed within solitary populations cannot explain reproductive isolation between the species pairs, at least for this single trait. We cannot yet rule out an effect of intraspecific assortment based on another as-yet unidentified trait. Certainly, a number of other traits influence female mate choice in this species (Milinski and Bakker, 1990; Milinski, 2003; McKinnon et al., 2004), and mate preferences are known to reduce interbreeding between parapatric and allopatric populations (Jones et al., 2006; Vines and Schluter, 2006; Eizaguirre et al. 2010), and between the sympatric species pairs (Rundle and Schluter, 1998; Boughman 2001; Rundle, 2002). The species pairs are more divergent for other phenotypic characters such as standard length (\( \Delta \approx 2 \)), body depth (\( \Delta \approx 3.2 \); Day et al., 1994), but even these traits do not approach the more than five standard deviation differences required for intraspecific assortment to have a
Case study 2: Darwin's finches

There is evidence of assortative mating with respect to beak size within several populations of Darwin’s Finches (Boag and Grant, 1978; Boag, 1983). For example, in the medium ground finch, Geospiza fortis, there is a positive correlation between bill length, bill width, or bill depth of mated pairs (r ranges from 0.16 to 0.42). Stronger assortment (up to r = 0.74) has been observed in a phenotypically bimodal population of G. fortis on Santa Cruz Island (Huber et al., 2007), but this bimodality obscures the taxonomic status of this population, and so it is ambiguous whether this is a measure of intraspecific assortment. If we consider the upper range of assortment (r ≈ 0.4) within G. fortis, a given pair of species would have to be 5.4 standard deviations apart to be 95% isolated, 7.2 SD apart to be 99% isolated, or 9 SD apart to be 99.9% isolated. Note that we do not have concurrent data on relative abundance of species on each island, so we assume f1 = 0.5.

For comparison, phenotypic divergence (Δ) in upper beak length between G. fortis and co-occurring congeners is 2.8, 4.1, 4.95, and 5.9 standard deviations (G. difficilis, scandens, fuliginosa, and magnirostris respectively). Assuming r = 0.4, the average Δ between G. fortis and each congener listed above would be sufficient to yield reproductive isolation strengths of 72% (G. difficilis), 86% (G. scandens), 93% (G. fuliginosa), and 97% (G. magnirostris). Although hybrids are occasionally reported among Geospiza species, the actual reproductive isolation between most of these species pairs is higher than the values predicted based on intraspecific assortment (Grant, 1986). We therefore infer that the intraspecific assortment in G. fortis is an insufficient explanation for species isolation between G. fortis and most or all of its co-occurring congeners. It is plausible that assortment contributes to isolation in combination with other forms of species recognition, or that intraspecific assortment acts on multiple independent traits (Podos, 2001) which jointly can generate stronger reproductive isolation between species.

The case of G. fortis is fairly representative of interspecific divergence in Darwin’s finches. Using published data on mean beak morphology measurements for multiple Geospiza species on multiple islands (Grant et al., 1985), we calculated Δ for all co-occurring pairs of Geospiza species on each island (Fig. 3; limited to species and islands with data in Grant et al., 1985). For example, Δ averages 6.16 (SD = 3.62; Fig. 3A) for upper mandible length, 4.56 (SD = 3.28; Fig. 3B) for upper mandible length, and 6.52 (SD = 4.43; Fig. 3C) for lower mandible width. Thus, the majority of co-occurring Geospiza species pairs are not sufficiently divergent for intraspecific assortment to generate >99% reproductive isolation, which would require Δ > 7 (Fig. 3). Lesser divergence can impart weaker reproductive isolation, but we would expect to see a correspondingly high rate of hybridization. Given the caveats described above, we tentatively conclude that intraspecific assortment based on beak morphology by itself is unable to explain reproductive isolation among a large fraction of Geospiza species, and so additional isolating mechanisms must be involved – either distinct species-recognition cues (e.g., song) or else multiple independent phenotypic traits subject to assortment. There are highly divergent species pairs (Fig. 3) where intraspecific assortment could plausibly drive essentially complete reproductive isolation. However, additional species recognition cues may also be the primary cause of reproductive isolation between these more divergent species pairs.

3 Discussion

A long-standing question is whether mating behaviors used to choose among conspecifics are also responsible for reproductive isolation between species (Ryan and Rand, 1993). Positive assortative mating, which is widespread in nature (Jiang et al., Manuscript), is an obvious candidate for such a dual-function behavior. A preference for phenotypically similar mates can simultaneously generate assortative mating within a population, and reduce the probability of mating with phenotypically divergent populations. This logic is invoked in numerous theoretical models, which assume that the evolution of intraspecific assortative mating leads to isolation between phenotypically divergent subpopulations (Dieckmann and Doebeli, 1999; Gavrilets, 2004). Our results confirm that strong reproductive isolation can arise from the combination of phenotypic divergence and intraspecific assortative mating. However, this
Fig. 3  The magnitude of phenotypic divergence, $\Delta$, between co-occurring species of Darwin's finches, for three traits (upper mandible length, upper mandible depth, and lower mandible width)

Vertical dashed lines indicate the magnitude of divergence required to attain reproductive isolation levels of 95%, 99% and 99.9%, assuming that finches typically exhibit strong assortment, comparable to the higher values observed within $G. fortis$ populations ($r \approx 0.4$) and assuming equal abundance of each species per pair. The strength of reproductive isolation is weaker (dashed lines shift to the right) if assortment is weaker or if the focal species is relatively rare. We used published values of sex-specific trait means and standard deviations for $Geospiza magnirostris$, $G. fortis$, $G. filigiosa$, $G. difficilis$, $G. scandens$, and $G. conirostris$ from 24 islands in the Galapagos archipelago (Grant et al. 1985) to calculate the divergence between each pair of species on a given island, $\Delta_{1,2} = \frac{1}{1/2(S_{1-females} - S_{1-males})} \frac{1}{1/2(S_{2-females} - S_{2-males})}$. The same species contributes to multiple species pairs on each island, and the same species pairs occur on multiple islands. However, because a given species' morphology differs among islands, we present the distribution of $\Delta$ for all species pairs and all islands.

Intuitive result only holds for substantially divergent populations. A within-species strength of assortment of $r = 0.5$ is as strong or stronger than what is seen in most natural populations (Jiang et al., Manuscript). Given that value, populations that are only a few standard deviations apart can achieve only limited reproductive isolation arising from assortment on a single trait axis. A future task would be to model the extent of introgression arising from such limited reproductive isolation. This task would require additional limiting assumptions.
about the genetic architecture and selection acting on the trait used for assortment.

Several caveats should be kept in mind regarding these results. First, our calculations only apply to assortative mating arising from absolute mating preference function (eq. 3) expressed in one sex (Lande, 1981). This is a widely used mate choice function in evolutionary theory. However, positive assortative mating within species may arise from several other behavioral processes. Assortative mating can arise from mutual directional preferences if, for example, females systematically prefer larger males (regardless of their own phenotype), and males systematically prefer larger females. Large males and large females will pair up, leaving smaller individuals to pair with each other, generating a trait correlation between mates. Assortative mating via mutual directional mate preferences could actually increase (or reduce) hybridization rates relative to random mating, if both sexes of one species prefer (reject) the higher trait values of the other species. Assortment can also occur if a phenotypic trait affects the location or timing of mating. The resulting correlation between mates’ trait values does not entail mate preferences as modeled in this paper. However, if both species exhibit similar trait-dependent habitat choice or phenology then the results presented here may also apply to assortment via spatial or temporal co-segregation. It is not known whether the many empirical cases of assortative mating within populations (Jiang et al., in revision) are due to absolute mating preference functions or other mechanisms.

A second caveat is that we assume that only a single phenotypic trait axis is subject to assortative mating. If females select similar males along multiple independent axes, reproductive isolation may be substantially stronger than we would expect based on one trait. It therefore becomes important to know the dimensionality of traits subject to assortative mating within populations. At present this dimensionality is unknown, but comparative study of adaptive radiations suggest that relatively few independent trait axes (typically dimensionality of 2 or less) are responsible for sexual isolation among species (Hohenlohe and Arnold 2010). The model we present can be extended to multiple independent traits under assortative mating: the probability of hybridization depends on the strength of isolation arising from assortment on each of $j$ different trait axes . $P_H = \prod_j (1 - P_{ij})$ In general, this hybridization rate will be lower as more independent traits are subject to assortative mating. Future work could extend this to assortment along multiple correlated trait dimensions.

A third caveat is that we focus on the level of unidirectional reproductive isolation arising from assortative mating within one species. The reciprocal strength of isolation (arising from mate choice by species 2 females) will of course depend on the level of assortment within species 2. Consequently the total hybridization rate, counting offspring from either reciprocal cross direction, would depend on the level of assortment within each species. Focusing on one species is justified because the hybridization rate will tend to depend most strongly on whichever species exhibits the weakest intraspecific assortment. Interestingly, inequalities in the strength or dimensionality of intraspecific assortment could generate asymmetries in the parentage of hybrids and thereby underlie directional introgression between species. However, in the present model we do not track the population genetic outcome (e.g., introgression) of a given level of reproductive isolation.

A final caveat is that our model presumes a particular causal relationship between intraspecific assortative mating and reproductive isolation between species, but this causation could be reversed. For example, reproductive character displacement (e.g., to avoid producing sterile or inviable hybrids) can drive evolution of both divergent male signaling traits and female preferences (Servedio and Kirkpatrick, 1997; Rundle and Schluter, 1998; Kirkpatrick, 2001; Servedio and Noor, 2003; Ortiz-Barrientos et al., 2004; Hoskin et al., 2005; Bank et al., 2012). Selection for choosier females, who discriminate against heterospecifics, might incidentally generate assortative mating as those females also discriminate against phenotypically divergent conspecific males. If this reversed causation is correct, then we would expect assortative mating to be strongest in populations experiencing reproductive character displacement, and weak or absent in populations that do not coexist with congeners.

In conclusion, our model confirms that intraspecific assortative mating, which is widespread in nature, can generate reproductive isolation between divergent populations. As shown above, intraspecific mate choice behaviors may be sufficient to explain reproductive isolation between species in some co-occurring species pairs given sufficient intraspecific assortment and/or interspecific divergence. The potential for reproductive isolation via intraspecific positive assortative mating can be evaluated for any given case study, simply by measuring assortative mating within one or both mem-
bers of a species pair, the phenotypic divergence between the species, and the rate of hybridization. For a number of empirical case studies where assortative mating and phenotypic divergence are known, it appears that co-occurring species are often too similar, so assortment alone (based on a single trait) would generate unrealistically high frequencies of hybrids (e.g., Fig. 3). We conclude that in many species pairs one must invoke additional isolating barriers to explain reproductive isolation between species. (Candolin 2003; Hankison and Morris 2003). These additional barriers may include assortment based on multiple independent trait axes, or species-recognition traits/behaviors that are not used in choosing among conspecifics.

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